1995

Umingmakstrongylus pallikuukensis gen. nov. et sp. nov. (Nematoda: Protostrongylidae) from Muskoxen, *Ovibos moschafus*, in the Central Canadian Arctic, with Comments on Biology and Biogeography

Eric P. Hoberg
United States Department of Agriculture, Agricultural Research Service, geocolonizer@gmail.com

Lydden Polley
University of Saskatchewan, lydden.polley@usask.ca

A. Gunn
Government of the Northwest Territories

J. S. Nishi
Government of the Northwest Territories

Published in CANADIAN JOURNAL OF ZOOLOGY 73 (1995), pp. 2266-2282.

Umingmakstrongylus pallikuukensis gen.nov. et sp.nov. (Nematoda: Protostrongylidae) from muskoxen, *Ovibos moschatus*, in the central Canadian Arctic, with comments on biology and biogeography

E.P. Hoberg, L. Polley, A. Gunn, and J.S. Nishi

Abstract: ***Umingmakstrongylus pallikuukensis*** gen.nov. et sp.nov. is established for a protostrongylid nematode in muskoxen, *Ovibos moschatus*, from the Kitikmeot Region (central Arctic) of the Northwest Territories, Canada. It is distinguished from *Cystocaulus* and other Muelleriinae by characters that include the following: males: deeply incised, bilobed bursa, independent externodorsal rays, telamon composed of distal transverse plate, absence of falcate crurae, and spicules not distally split; females: absence of provagina; and first-stage larvae: presence of three cuticular folds on the tail. The great length of females (468 mm) and males (171 mm) is exceptional among the Protostrongylidae. Pathognomonic lesions include well-defined cysts dispersed through the lung tissue (maximum diameter 40 mm) containing adult and larval parasites in a dense matrix. Transmission involves a molluscan intermediate host, as indicated by experimental infections in the slug *Deroceras reticulatum*. The parasite is apparently restricted in its geographic distribution and has been found only in a population of muskoxen northwest of Coppermine, N.W.T. This may be indicative of a relictual host–parasite assemblage that has existed since the Pleistocene. The pathogenicity, high prevalence, and intensity of infection in the Coppermine herd suggest that the occurrence of *U. pallikuukensis* has implications for the management of muskoxen in the Holarctic region.

Résumé : Le nom ***Umingmakstrongylus pallikuukensis*** gen.nov. et sp.nov. est proposé pour désigner un nématode protostrongylidé parasite d'*Ovibos moschatus* dans la région de Kitikmeot (centre de l'arctique) dans les Territoires du Nord-Ouest, Canada. Le parasite se distingue de *Cystocaulus* et des autres Muelleriinae par certaines caractéristiques du mâle : bourse bilobée, très découpée, rayons externodorsaux indépendants, telamon composé d'une plaque transverse distale, absence de crura falciformes, spicules entiers à leur extrémité distale; chez les femelles, il n'y a pas de provagin; chez les larves de premier stade, la queue compte trois replis cuticulaires. La longueur très grande des femelles (468 mm) et des mâles (171 mm) est exceptionnelle chez un protostrongylidé. Les lésions pathognomoniques consistent entre autres en des kystes bien visibles dans le tissu pulmonaire (diamètre maximal de 40 mm), kystes contenant des parasites adultes ou larvaires dans une matrice compacte. La transmission se fait par l'intermédiaire d'un mollusque, comme l'ont démontré les infections expérimentales chez la limace *Deroceras reticularum*. Le parasite semble avoir une répartition géographique limitée et n'a été trouvé qu'au sein d'une population de Boeufs-musqués habitant au nord-ouest de Coppermine, Territoires du Nord-Ouest. Il est possible que cette association représente une relation hôte–parasite relicte qui remonte au Pléistocène. La fréquence élevée, la gravité et la nature pathogène des infections chez le troupeau de Coppermine indiquent que la présence d'*U. pallikuukensis* est une variable dont il faudra tenir compte lors de l'aménagement des troupeaux de Boeufs-musqués dans la région holarctique. [Traduit par la Rédaction]

Received May 10, 1995. Accepted August 10, 1995.

E.P. Hoberg. United States Department of Agriculture, Agricultural Research Service, Biosystematics and National Parasite Collection Unit, BARC East No. 1180, 10300 Baltimore Avenue, Beltsville, MD 20705, U.S.A. (e-mail: ehoberg@ggpl.arsusda.gov).
L. Polley. Department of Veterinary Microbiology, Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, SK S7N 5B4, Canada.
A. Gunn. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, NT X1A 2L9, Canada.
J.S. Nishi. Department of Renewable Resources, Government of the Northwest Territories, Coppermine, NT X0E 0E0, Canada.

Can. J. Zool. **73**: 2266–2282 (1995). Printed in Canada / Imprimé au Canada

Introduction

Metastrongyloid lungworms of the family Protostrongylidae Leiper, 1926 have been only sporadically reported in ruminant hosts from high latitudes of the Holarctic region (Boev 1975) and records in muskoxen (*Ovibos moschatus* (Zimmermann)) are rare. In the Palearctic region, protostrongylids documented in herds established in Scandinavia are considered to have been derived from contact with other wild and domestic ruminants following introduction (Alendal and Helle 1983; Holt et al. 1990; Stéen et al. 1994). In contrast, in the Nearctic region, Gunn and Wobeser (1993) found an apparently undescribed and pathogenic protostrongylid, thought to be similar to *Muellerius capillaris* (Mueller, 1889) (first-stage larva with dorsal spine). The parasite is prevalent in an isolated and localized herd of muskoxen that winters along the valley of the Rae and Richardson rivers northwest of Coppermine, Northwest Territories, Canada. This nematode constitutes the focus of our study.

In June 1988, lungs and cysts containing specimens of an exceptionally large protostrongylid were collected from an adult female muskox near the Rae River, N.W.T. (ca. 68°17′N, 116°05′W) (Gunn et al. 1991). Thirty macroscopic cysts containing adult worms and first-stage larvae in a dense matrix were recovered and counted at the time of necropsy. Subsequently, two radio-collared adult females were found dead (one from presumed predation by a barrenground grizzly bear, *Ursus arctos* Linnaeus, and the other from pneumonia); both had in excess of 50 similar cysts in the lungs.

The discovery of this apparently unknown species of protostrongylid prompted more detailed study that resulted in the examination of 53 pairs of lungs from hunter-killed animals in 1989–1990, and collection of fecal specimens during July–August 1990 on summer range occupied by muskoxen north of the Rae-Richardson Valley, N.W.T. (A. Gunn, unpublished data). These observations established that there was a high prevalence of this nematode: 92.5% of 53 adult muskoxen, based on examination of lungs, with a maximum of 258 cysts per host, and 91% of 88 randomly collected fecal samples (Gunn and Wobeser 1993). The high prevalence and apparent pathogenicity of this parasite suggested that it could affect the population dynamics of these muskoxen. Since the original collections in 1988, this protostrongylid has consistently been found in hunter-killed muskoxen from the valleys of the lower Rae and Richardson rivers, but is apparently absent in animals from other herds in the Canadian Arctic (Gunn et al. 1991; unpublished pathology reports, Western College of Veterinary Medicine).

Adult males and females collected during this period proved insufficient for studies in systematics. However, first-stage larvae from lungs and feces had a characteristic dorsal spine, suggesting their similarity to *Muellerius*, *Cystocaulus* Schulz, Orlow, and Kutass, 1933, and other genera of protostrongylids (Gunn and Wobeser 1993). Consequently, in April 1994, collections of new material were conducted in the area adjacent (60 km northwest) to the settlement of Coppermine. The complete adult nematodes, additional cephalic and caudal extremities, and larvae that were collected are the basis for the diagnosis of a new genus and description of a previously unknown species of protostrongylid. Additionally, in view of the potential management implications of this parasite in *O. moschatus*, aspects of parasite biology, potential transmission patterns, host range, and historical biogeography are considered.

Materials and methods

Initial collections; Rae and Richardson River valley, 1988–1990

Cysts containing adult and larval parasites were initially collected from the lungs of a female muskox north of the Rae River, N.W.T., in 1988: Western College of Veterinary Medicine (WCVM) Pathology No. N88-3686. Later, specimens were processed from some of 53 muskoxen taken by hunters in 1989 and 1990 (Gunn et al. 1991): WCVM N89-4135 and 4136 in November 1989 and WCVM N90-0972, 3185, 3199, and 3200 in April 1990. Additional animals collected in 1991 (WCVM N91-0499) and 1992 (N92-0789) were also examined. Cysts were excised and fixed in buffered 10% neutral formalin for gross and histological examination. In 1993 one of us (L.P.) recovered a series of caudal and cephalic extremities of males and females as well as first-stage larvae from the material collected in 1991 and 1992. Additionally, details of larval and adult morphology (from transverse sections in situ) and localization in the host were determined histologically from cyst and lung tissue collected in 1990 (WCVM N90-972 and N90-3185). Previously fixed specimens were embedded in paraffin, sectioned at 6 μm, stained in hematoxylin and eosin, and mounted in Permount.

Field collection at Cox Lake, N.W.T., 1994

Collection was conducted under Wildlife Research Permit No. 1023 issued by the Government of the Northwest Territories. On 12 April 1994, two adult bull muskoxen (COMX-001 and 002) were collected at Cox Lake (67°54′N, 116°38′W), along the drainage of the Rae and Richardson rivers. Infected animals were identified prior to collection by Mr. Allen Niptanatiak, based on the observation that they appeared weak, and bled from the nose when stressed by running. Animals were necropsied in the field, an array of biological specimens being taken for later evaluation (jaws and skull for determination of age, kidney fat for determination of condition, rumen contents, rectal feces, and parasitological samples). The entire lungs and abomasum from each animal were collected, placed in an insulated box together with "Safe and Warm™ Reusable Instant Heat Packs" (McCarthey and Sons, Calgary, Alberta) to prevent immediate freezing. "Heat Packs" will generate a temperature of 52°C for at least 30 min, after which they cool at a rate determined by the surrounding insulation and ambient temperature. The air temperature at the site of collection and during the return trip was −20 to −30°C. Specimens were transported to the laboratory for examination, which occurred within 5 h of collection. The carcasses and skins were transported back to the settlement of Coppermine.

In the laboratory, cysts present in the lungs were counted and measured. These specimens were processed as follows: for COMX-001: both lungs were immediately stored at 4°C for later transport to the University of Saskatchewan; for COMX-002: some lung tissue with cysts was fixed immedi-

ately in 10% formalin. Some unfixed cysts were dissected and incubated in physiological saline at near 37.5°C to enhance the release of adult worms. Others were dissected in physiological saline for immediate collection of adult parasites. Adult nematodes were carefully removed from the matrix of the cysts with the aid of a stereo dissecting microscope at magnifications of 10–60×. Specimens were later simultaneously killed and preserved by immersion in steaming hot 70% ethanol. This work extended from about 20:30 on 12 April until about 15:30 on 14 April, at which point the adult worms were beginning to die and degenerate; only entire parasites or fragments of worms fixed while alive were used for the description. First-stage larvae collected from cysts were fixed in 10% neutral buffered formalin or preserved in 70% ethanol.

Baermann separations were initiated for recovery of first-stage larvae from lung tissue (in saline) and rectal feces (in tap water) beginning at 20:30 on 12 April. Separations were conducted using 150 mm wide funnels, and a light source overhead to provide heat; tissue or feces was suspended in a cheesecloth bag. Lung tissue was sampled from COMX-002; examinations of Baermann apparatus were conducted after 24 h, and the separation was terminated at 10:30 on 14 April. At that time a second separation from additional lung tissue was run until 09:00 on 15 April. All larvae from lungs were stored in saline and refrigerated at 4°C. Feces from COMX-001 (127.7 g) and COMX-002 (126.5 g) were suspended intact in cheesecloth in water. Larvae extracted from the Baermann apparatus were stored in tap water at 4°C.

In November 1994, four additional muskoxen were collected 15 km northwest of Cox Lake: two adult cows older than 5 years (Nos. 94-Mx-10 and 56) and a 2.5-year-old male and a 3.5-year-old female (Nos. 94-Mx-18 and 11, respectively). In these animals, only the cysts were counted. First-stage larvae were collected from the lungs and feces for studies of life history, which are in progress. Adult and larval nematodes from these hosts were not used in the current description, but were morphologically consistent with those previously collected.

Laboratory procedures at the University of Saskatchewan, 1994

Refrigerated specimens of whole lungs, cysts, and larvae were transported from Coppermine to WCVM, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, on 15–16 April. Gross examination and photography of the lungs of COMX-001 were completed. Baermann separations were initiated for collection of additional first-stage larvae from the lungs and rectal feces. Larvae were collected from the lungs after 24 h and from the feces after 24 and 48 h, and maintained suspended in water at 4°C in 1-L glass flasks.

First-stage larvae from the lungs and feces were used to establish experimental infections in slugs (*Deroceras reticulatum* (Müller, 1774)), raised from eggs and known to be parasite-free. The following protocol was used: slugs were fasted for a minimum of 3 h, then 6–10 slugs were placed on No. 3 Whatman filter paper presaturated with a suspension containing larvae in 7-cm petri dishes, which were shaken gently to ensure that the slugs remained in contact with the filter paper. Individual slugs were exposed as follows: each slug was grasped carefully with forceps and inverted to expose the foot, and larval suspension was dropped from a Pasteur pipette onto the foot of each slug; this procedure was repeated every 30 min for a minimum of 3 h per day for 5 days. Each day of the infection began with the fasting period; between procedures, slugs were maintained in small plastic boxes with small amounts of lettuce, carrots, and chalk. At the conclusion of the infection protocol, slugs were maintained at room temperature (estimated 20°C) on 50% autoclaved potting soil and 50% vermiculite in ventilated plastic boxes and fed as specified above.

Larvae were collected from slugs following pepsin digestion, as follows: slugs were cut into small pieces and placed in a pepsin solution (7 g of 1 in 10 000 pepsin and 8 mL 1 M HCl in 1 L of water); the suspension was agitated in a water bath at 37°C for approximately 1 h and then placed in a petri dish with a grid and examined for larvae with a dissecting scope at 250×. Individual larvae were removed by pipette and fixed in 10% formalin at 70°C. Larvae were recovered from slugs infected daily over 5 days (18–22 or 25–29 April 1994) and processed for recovery on 1 June or 25 May 1994, respectively. Third-stage larvae on which measurements were based were derived from slugs infected from 41 to a maximum of 45 days.

Laboratory procedures at USDA, 1994

At the Biosystematics and National Parasite Collection Unit, U.S. Department of Agriculture (USDA), Beltsville, Maryland, specimens of nematodes collected in 1994 were transferred to a solution of 70% ethanol, 5% formalin, and 2% glycerine. Specimens from previous years were stored in buffered 10% formalin or in 70% ethanol. Adult nematodes were prepared as uncleared whole mounts in water, or were cleared in glycerine or phenol–alcohol and examined using differential interference contrast microscopy (ICM). Transverse sections cut by hand with a cataract knife were prepared from adult males and females and first- and third-stage larvae for examination of the cuticle and disposition of chords and other internal structures. Two cephalic extremities of adult nematodes were prepared for scanning electron microscopy (SEM). These were dehydrated through a series of ethanol solutions, critical-point dried, mounted on stubs, and sputter-coated with gold–palladium. SEM was conducted with a Hitachi S-5700 microscope at 10 kV with magnifications from 350 to 11 000 ×. Larvae were examined with oil-immersion and ICM optics at 1600× magnification; specimens were not cleared.

The following description is based on entire specimens and fragments of the cephalic and caudal extremities of male and female worms. The following adult specimens were measured: 8 entire males, including the holotype, and 24 caudal extremities; additional males examined but not measured include 8 caudal extremities (total of 40 in male type series); 1 entire female (allotype) and 20 caudal extremities; additional females examined but not measured include 3 caudal extremities (total of 24 in female type series). Cephalic extremities, in which the sex of the worm could not be unequivocally determined, included 43 specimens in the type series and 2 specimens examined by SEM (total of 45). First-stage larvae collected from lung tissue and rectal feces using Baermann separation and third-stage larvae derived from experimental infections in the slug *D. reticulatum* were

studied. Consistency in meristic and structural characters in first-stage larvae from lungs and feces was confirmed; data presented in the description are for first-stage larvae from the lungs. Measurements of adult nematodes and larvae are presented in micrometres unless specified otherwise. In the description, the sample size (*n*) is followed by the range and mean, with the standard deviation in parentheses. The type series and voucher specimens were deposited in the collections of the Canadian National Museum of Nature (CMNP), Ottawa, Ontario, and in the U.S. National Parasite Collection (USNPC), USDA, Beltsville, Maryland.

Other specimens examined

Voucher material examined: *Cystocaulus ocreatus* (Railliet and Henry, 1907) (type for genus), USNPC 37845, recorded as *C. nigrescens*, which is a synonym according to Boev (1975), in *Ovis aries* Linnaeus from Alma-Ata, former USSR; *Cystocaulus vsevolodovi* Boev, 1946, USNPC Nos. 37850 and 37852, in *Capra sibirica* Pallas from Chuiakskii, Dzhuniarsk, Ala Tai, former USSR; and *Cystocaulus* sp., USNPC 69575, in *Ovis aries* from Germany. *Muellerius capillaris* (Mueller, 1889) (type for genus), USNPC No. 78504, in *Ovis canadensis canadensis* Shaw from South Dakota, U.S.A.; USNPC No. 34004, in *Capra hircus* Linnaeus, from Puerto Rico; USNPC No. 33169, in *Ovis aries* from Washington, D.C.; and *Muellerius* sp., USNPC No. 66852, in *Ovis aries* from Virginia, U.S.A. Most specimens studied for comparative purposes were in poor condition.

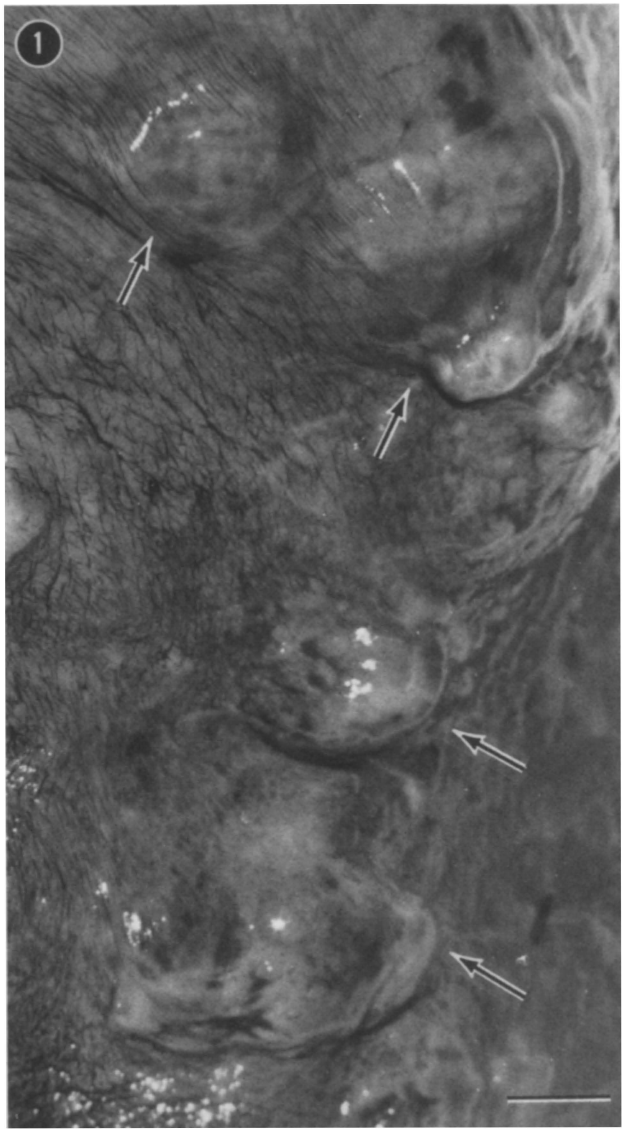
Results

Numerous reddish brown adult protostrongylid nematodes were found in large cysts in the lungs of 2 adult male muskoxen collected in April 1994 (Figs. 1–5). In COMX-001 there were 41 and 47 cysts and in COMX-002 81 and 68 cysts in the right and left lung, respectively. Cysts were also counted in both lungs from muskoxen collected in November 1994: 2 females older than 5 years (94-Mx-10 with 159 cysts and 94-Mx-56 with 169 cysts), a 2.5-year-old male (94-Mx-18 with 11 cysts), and a 3-year-old female (94-Mx-11 with 26 cysts).

Cysts (Fig. 1) were located in the dorsal parts of the cranial, middle, and caudal lobes of each lung. Cysts were visible and palpable on the surface of the lung parenchyma and were also present deep in the lung tissue, had spherical to irregular margins, and measured 9–40 mm in greater diameter ($n = 50$) (Fig. 2). Based on preliminary observations, a maximum of 2 or 3 females and >5 males may reside within each cyst (Fig. 3).

On histological examination, adult nematodes were found within cysts separated from surrounding lung tissue by a capsule of connective tissue (Figs. 4 and 5). Cysts were filled with a dense yellowish green spongy matrix composed of exudate, developing eggs, and larvae, as well as fully formed first-stage larvae. Within the matrix, adult nematodes were tightly coiled and entwined; first-stage larvae were also present in bronchioles adjacent to the cyst (Figs. 4 and 5). In apparently well-circumscribed regions in some cysts the matrix contained only degenerate nematodes (Fig. 4). In addition, some cysts contained necrotic and mineralized debris and only degenerate parasites. Details of the pathology will be reported elsewhere.

Fig. 1. Infected lung, lateral view of caudal lobe, showing prominent cysts (arrows). Scale bar = 10.0 mm.

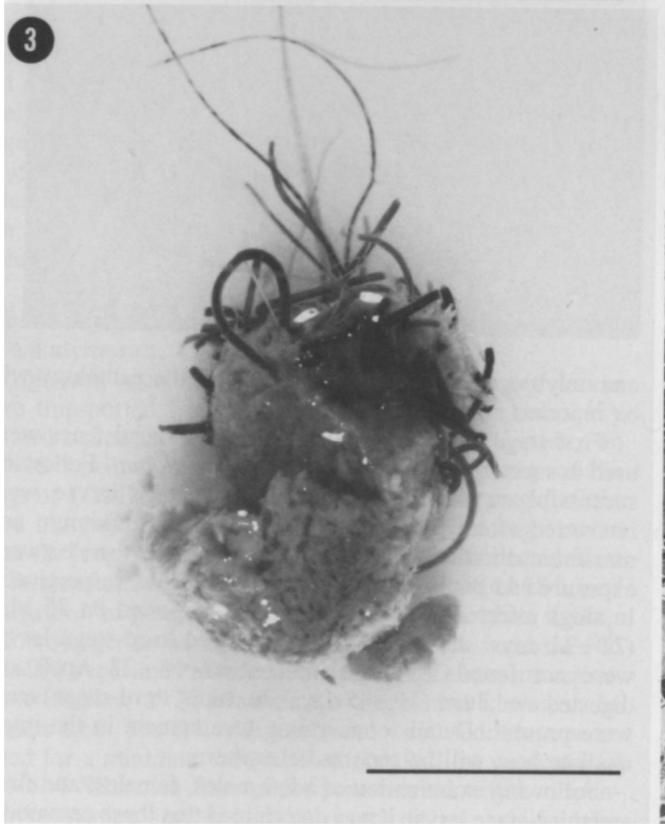


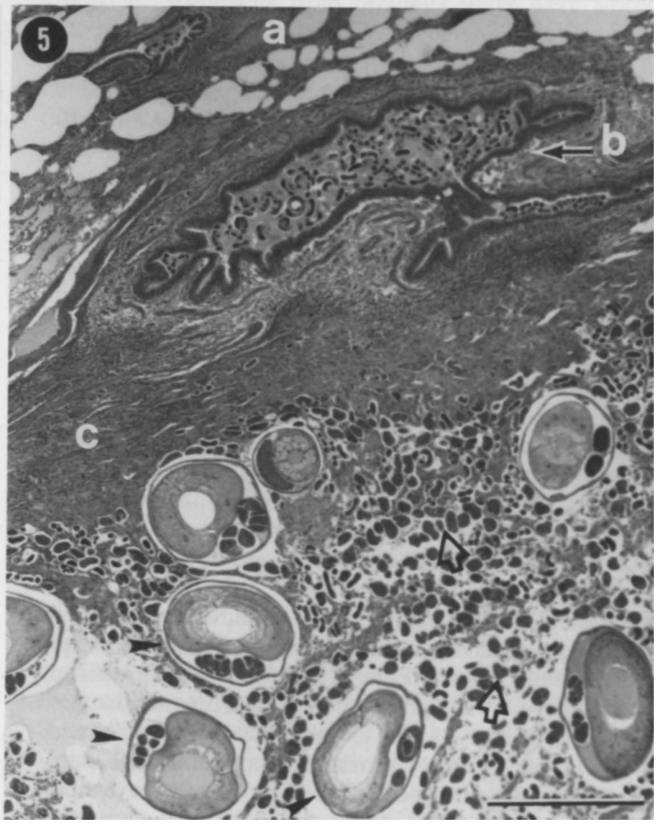
First-stage larvae from lung tissue and rectal feces were used to successfully infect *Deroceras reticulatum*. Following successful experimental infection, third-stage larvae were recovered after approximately 40 days, the minimum and maximum duration of infection (based on the time between exposure and digestion) being 27 and 45 days, respectively. In slugs infected on 25–29 April and digested on 25 May (27–31 days' duration), fully developed third-stage larvae were not found. In slugs infected on 18–22 April and digested on 1 June (41–45 days' duration) third-stage larvae were present. Details concerning development in the intermediate host will be reported elsewhere.

Following examination of adult males, females, and first- and third-stage larvae it was determined that these nematodes represented a previously unrecognized genus and species within the Protostrongylidae. The generic diagnosis and description of the species presented herein are based on


2


4
5


3


5
a
b
c

Figs. 2–5. Gross lesions and histological preparations of protostrongylids from muskoxen. Fig. 2. Internal structure of typical cysts in lung tissue, shown in a thick transverse section cut by hand; note the dark adult nematodes (arrowheads) entwined in a dense pale matrix (arrow). Scale bar = 10.0 mm. Fig. 3. Contents of an excised cyst, showing adult nematodes embedded in a matrix. Scale bar = 10 mm. Fig. 4. Histological section through a cyst stained with hematoxylin and eosin, showing the distribution of adult nematodes in a matrix (arrowheads) and a well-delineated area of the cyst (arrows) containing degenerate parasites; "5" with an arrow indicates the location of Fig. 5. Scale bar = 5.0 mm. Fig. 5. Histological section through the peripheral region of a cyst, showing numerous adult nematodes in transverse section (arrowheads), eggs, and first-stage larvae within the matrix (open arrows); note the cyst wall (*c*), an adjacent bronchiole containing first-stage larvae (*b*), and surrounding alveolar tissue (*a*). Scale bar = 500 μm.

adults and first-stage larvae collected from naturally infected hosts and third-stage larvae derived from experimental infections of a putative molluscan intermediate host.

Umingmakstrongylus gen.nov.

DIAGNOSIS: Protostrongylidae, Muelleriinae, of exceptionally large dimensions. Male with bilobate, usually asymmetric bursa; origin of externodorsal rays independent of dorsal ray; stalk-like dorsal ray trilobate, with 6 papillae. Telamon reduced, composed of distal transverse plate. Gubernaculum well developed; capitulum with paired, arcuate, ventral ears or anchor piece enveloping spicules and paired dorsal ears directed distally over unpaired corpus; crura paired, fused proximally with corpus, distally crura with ventrally directed tooth-like projections but lacking prominent falcate dorsal feet. Spicules massive, long, with distinctive joint in posterior third; not split distally. Female lacking provagina. First-stage larva with prominent dorsal spine and 3 cuticular folds on tail. Parasites of ruminants; occurring in lung tissue within cysts.

Type and only known species: *Umingmakstrongylus pallikuukensis* gen.nov. et sp.nov.

HOST: Muskox, *Ovibos moschatus moschatus* (Zimmermann).

Umingmakstrongylus pallikuukensis sp.nov.
Figs. 6–34

General description

Protostrongylid nematodes of exceptional length; cuticle delicate, smooth, easily separated, with minute transverse striations; reddish brown to dark brown in life; intestine darkly pigmented. Cervical region weakly tapered (Fig. 6). Cephalic extremity bluntly rounded, (n = 47) 31–52 (41 ± 6.08) in diameter; triangular stoma bordered by prominent lateral amphids, 10 papillae of the outer circle including 4 paired dorsal and ventral and single laterals, and 6 pedunculate papillae of the inner circle (Figs. 8–10). Esophagus cylindrical, broadening at base, (n = 51) 494–757 (583 ± 53.84) long and 78–130 (102 ± 11.56) in maximum width, demarcated into short anterior muscular section and posterior glandular section; width of body at base of esophagus (n = 48) 143–286 (201 ± 41.64) (Fig. 13). Nerve ring an indistinct, diffuse narrow band, (n = 43) 104–226 (167 ± 27.95) from anterior. Cervical papillae minuscule, (n = 28) 106–374 (236 ± 58.53) and obscure excretory pore (n = 38) 109–425 (239 ± 63.45) from cephalic extremity near anterior to middle third of esophagus (Figs. 6, 7, and 13). Lateral chords massive, prominent, sinuous in cervical region (Fig. 12), with orange–brown pigmentation. Body, in transverse section, with paired ventral and massive, lateral chords, and 4 sublateral chords (Figs. 14 and 15).

Female

In allotype, length 468 mm, width of cephalic extremity 39, width at base of esophagus 242, maximum width attained in midbody 425. Specimen slightly contracted in anterior; esophagus 546 long and 91 wide at base; length of esophagus 0.12% of body length; cervical papillae 106, excretory pore 109, and nerve ring 117 from anterior; tail 95 long; vulva to tail tip 251, width at vulva 231; vagina 1725 and sphincter 117 in length.

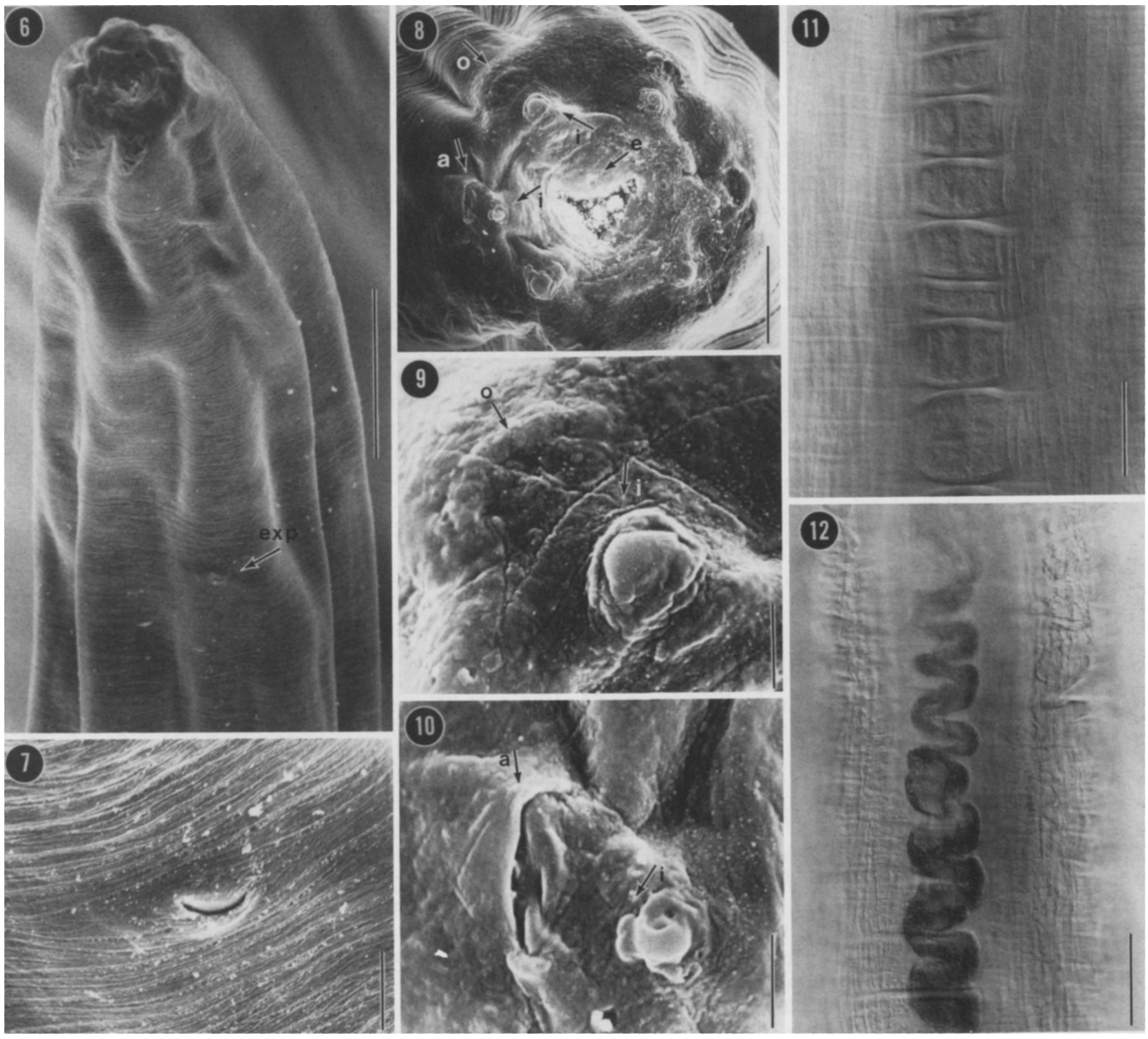
Based on 21 female tails including the allotype and 2 nearly complete specimens up to 384 mm in length (Figs. 16–20). Prominent hypodermal striae overlaying lateral chords, apparent in slightly contracted specimens, forming ladderlike pattern; extending from near level of esophagus in anterior to near margin of vulval protuberance (Fig. 11). Caudal region often flexed dorsally. Tail conical, with lateral phasmids near apex, often with minuscule papilla-like knob situated at tip; tail length (n = 20) 81–122 (100 ± 11.58). Anal aperture in semilunar fold; papilla-like pores, ventrolateral in position, opening slightly anterior to anus and posterior to vulva, with duct extending anteriad within massive lateral chord. Vulva with aperture on solid, knoblike protuberance, directed posteroventrally; cuticular fold extending dorsally across protuberance from anterior lip of vulva; membranous provagina lacking (Figs. 18–20). Distance from vulva to anus (n = 20) 117–247 (175 ± 34.51); from vulva to tail tip (n = 20) 205–338 (276 ± 40.06); width at vulva, determined with specimens in dorsoventral orientation, (n = 20) 143–205 (173 ± 24.22). Vagina voluminous, (n = 18) 1400–2100 (1709 ± 188.88) in length, extending anteriad from vulva to prominent sphincter (n = 19) 104–174 (124 ± 16.84) in length (Fig. 16). Uteri paired, prodelphic, proximal to vagina enveloped by sphincter (Fig. 17). Eggs, with delicate, friable shells, measured in utero and in cyst at morula stage, (n = 50) 99–125 (112 ± 6.32) long × 55–73 (64 ± 5.51) wide.

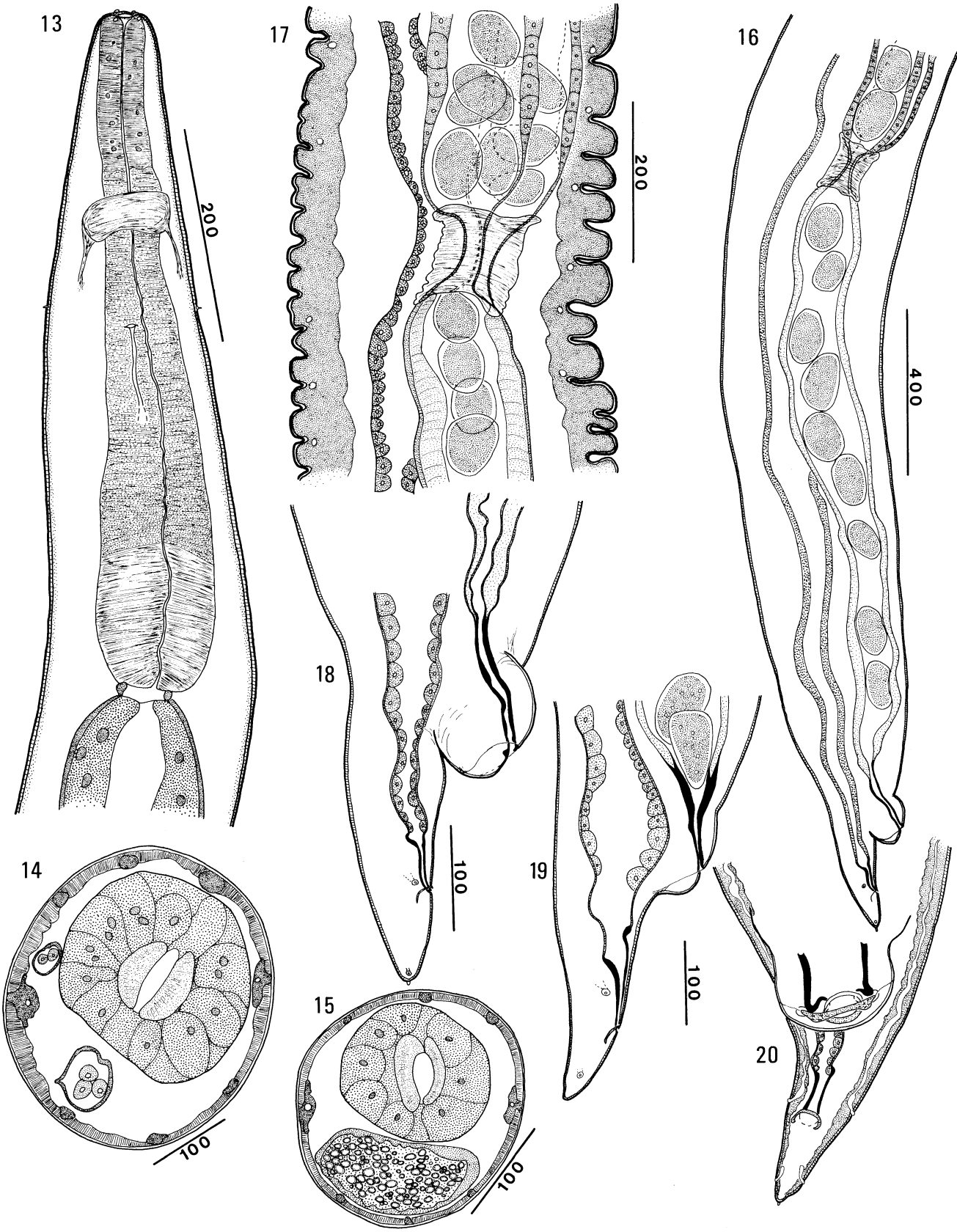
Male

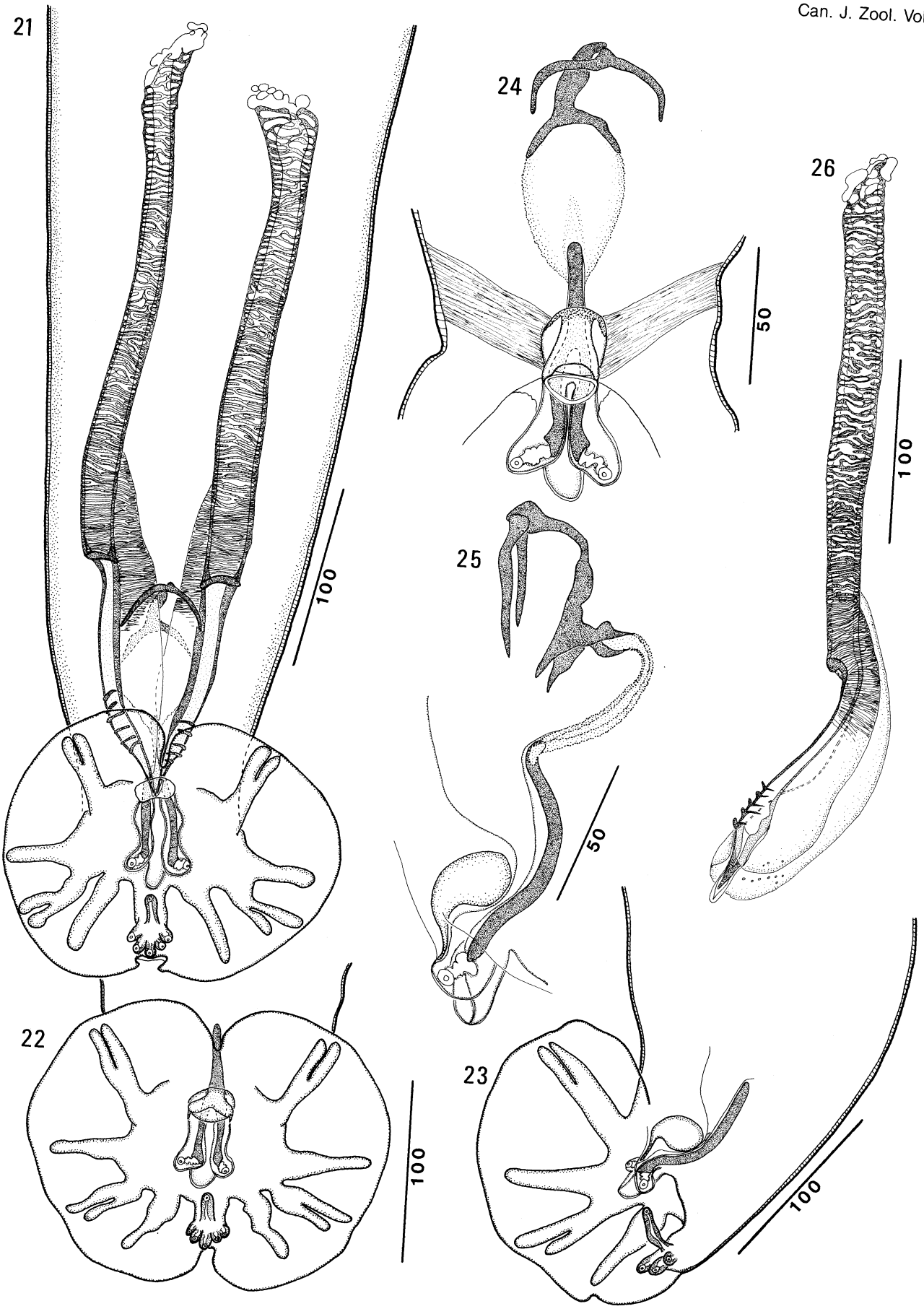
In holotype and 7 additional entire males: length (n = 7) 107–171 mm (145 ± 21.12); width of body at cephalic extremity 34–42 (38 ± 2.99), at base of esophagus 140–177 (154 ± 13.99); maximum width near midbody (n = 8) 237–286 (266 ± 15.72). Esophagus (n = 7) 520–624 (571 ± 36.42) long and 81–109 (95 ± 11.27) wide at base; length of esophagus 0.34–0.50% of body length. Nerve ring (n = 6) 159–216 (194 ± 23.30), cervical papillae (n = 6)

Figs. 13–20. *Umingmakstrongylus pallikuukensis* gen.nov. et sp.nov. Cephalic region, cuticular structures, and female characters. Fig. 13. Cervical region in ventral view, showing the positions of the excretory pore, cervical papillae, and nerve ring. Fig. 14. Female in cross section near the midbody; note 8 chords. Fig. 15. Male in cross section near the midbody. Fig. 16. Female tail, lateral view, showing the relative positions of the anus and vulva and the overall structure of the vagina and ovejector. Fig. 17. Proximal region of ovejector in ventral view, showing the uterine limbs, sphincter, and proximal vagina (anterior toward the top). Fig. 18. Tail in lateral view, showing the prominent vulval protuberance and perivulval pores. Fig. 19. Tail in lateral view, with relatively small vulval protuberance. Fig. 20. Tail in ventral view; note the position of the perivulval pores lateral and anterior to the anus.

Figs. 6–12. *Umingmakstrongylus pallikuukensis* gen.nov. et sp.nov. Fig. 6. Cervical region, showing position of the excretory pore (*exp*). SEM. Scale bar = 50.0 μm. Fig. 7. Excretory pore, showing orientation and structure. Scale bar = 5.0 μm. Fig. 8. Cephalic extremity, en face view, dorsal toward the top; note the positions of the inner (*i*) and outer (*o*) circles of papillae, amphids (*a*), and the orifice of the dorsal esophageal gland (*e*). Scale bar = 10.0 μm. Fig. 9. Structure of the outer (*o*) and inner (*i*) papillae. Scale bar = 2.0 μm. Fig. 10. Inner papilla (*i*) and amphid (*a*). Scale bar = 2.0 μm. Fig. 11. Hypodermal striae, in a slightly contracted female specimen. ICM. Scale bar = 50.0 μm. Fig. 12. Lateral chord, showing deep pigmentation and massive size. Scale bar = 50.0 μm.




13
200
17
200
16
400
18
100
19
100
14
100
15
100
20


21
100
24
50
26
100
25
50
22
100
23
100

Figs. 21–26. *Umingmakstrongylus pallikuukensis* gen.nov. et sp.nov. Male. Fig. 21. Caudal extremity with the bursa in ventral view; note the deeply incised asymmetric bursa, stalk-like dorsal ray with 6 papillae, and independent origins of externodorsal rays. Fig. 22. Bursa in ventral view, showing the symmetric lobes; gubernaculum and the distal transverse plate of the telamon. Fig. 23. Bursa in lateral view, showing the right lobe and the disposition of rays and papillae; the spicules and the capitulum of the gubernaculum are not shown. Fig. 24. Gubernaculum in ventral view. Fig. 25. Gubernaculum and the distal transverse plate of the telamon in lateral view. Fig. 26. Right spicule in lateral view, showing the prominent ctenidium-like ribs distally, the structure of the alae, and the trabeculae typical of the spongy column; note the cuticularized joint in the distal third.

230–338 (280 ± 41.21), and excretory pore (n = 7) 220–377 (291 ± 52.34) from anterior.

In holotype, 7 entire males, and 24 caudal extremities (Figs. 21–26): bursa rounded, deeply incised along posterior and anterior margins, distinctly divided into lobes, which may be asymmetric in size (Figs. 21–23); overall (n = 27) 104–169 (143 ± 15.06) in length, 169–229 (201 ± 14.81) in maximum width; body constricted at junction with bursa. Bursal rays generally approaching, and may attain, margin of bursal membrane. Ventroventral and lateroventral rays arise from common base, directed anteriad and isolated from other rays; tips of rays separated for nearly half their length. Lateral rays arise from common base, with externolateral rays isolated from relatively elongate medio- and posterolateral rays; tips of latter rays separate for greater than half their length. Externodorsal rays short, with origins independent of base of dorsal ray, not attaining margin of bursa. Dorsal ray relatively thick, distinctly stalk-like, elongate, (n = 31) 29–57 (39 ± 6.58) in length. Dorsal ray trilobed with 5 terminal papillae disposed in 2 lateral pairs and a median terminal papilla; single median pedunculate papilla, directed ventrally, situated on main stalk of ray anterior to apex and near level of trifurcation.

Telamon reduced, composed of independent distal transverse plate; proximal plate lacking (Figs. 24 and 25). Distal plate ovoid to oblong, slightly transversely elongate, (n = 32) 13–23 (17 ± 2.93) long × 21–31 (26 ± 2.85) wide; situated ventral and slightly anterior to cloacal aperture. Anterior margin of plate appears amorphous; ventrally 2 projections extend posterolaterally in a platelike structure crossing posterior margin of main body of telamon, in lateral view appearing as beak-like posteriad processes from the distal plate. Ventral projections of telamon extend into semilunar, ringlike support for the cloacal aperture, ventral to legs of gubernaculum. From level of cuticularized cloacal ring is a posteriad cuticular extension from telamon that surrounds ends of legs of gubernaculum and terminates in a trilobed membrane with a ventrally directed papilla in each of lateral lobes (Fig. 24). Median lobe lacks a papilla and is developed as a troughlike elongation that extends between legs of gubernaculum. Trilobed membrane situated ventral to dorsal lobe of bursa and surrounds cloacal orifice.

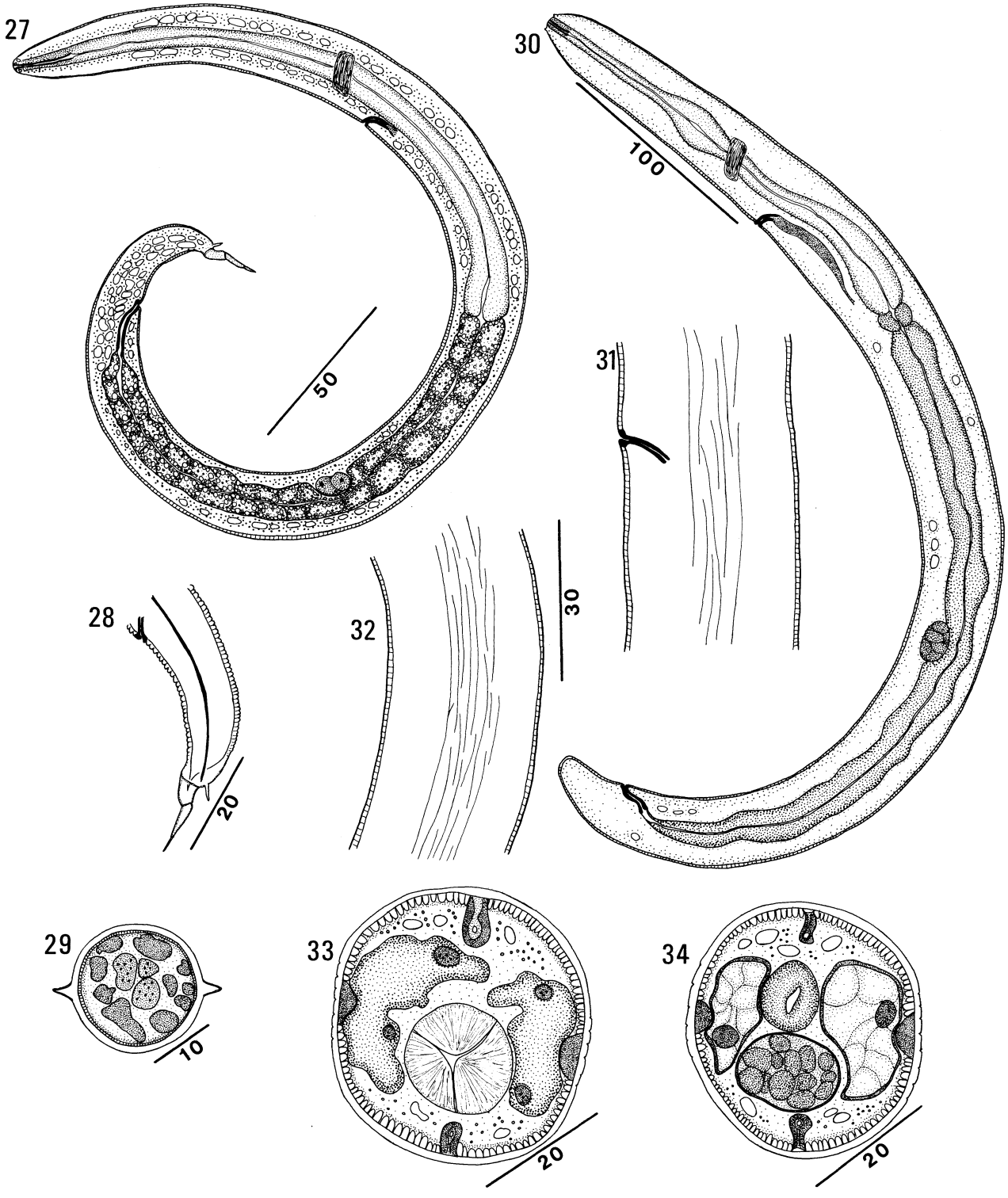
Spicules equal to subequal, yellowish brown, with distinct joint in posterior third demarcating anterior spongy column from heavily cuticularized alate distal region; not split distally (Figs. 21 and 26). Left spicule (n = 32) 328–431 (379 ± 28.85) long; anterior column 231–299 (257 ± 18.97); joint located at 64–72% (68 ± 2.19%) along length of spicule from capitulum; with (n = 30) 4–8 (6 ± 0.89) ctenidium-like ribs near tip of main shaft. Right spicule (n = 32) 341–463 (391 ± 27.99) long; anterior column 231–312 (261 ± 22.09); joint located at 62–70% (67 ± 2.17%) along length from capitulum; with (n = 30) 4–8 (5 ± 0.96) ribs near tip of main shaft. Spicule tips acute, without dorsal or ventral cuticularized processes associated with alae. Prominent alae, with well-developed trabeculae, originate slightly anterior to joint of spicules, expand posteriad to become balloonlike adjacent to tip of main shaft of spicule; larger dorsal ala extends to near cuticularized, acutely pointed tip of spicule.

Gubernaculum complex, with well-developed capitulum, corpus, and crura (Figs. 24 and 25); overall length (n = 32) 109–156 (139 ± 11.83); length of crura 29–52 (41 ± 5.18) and of corpus 73–117 (98 ± 11.94). Capitulum cuticularized, with prominent arcuate anchor piece situated ventrally and enveloping spicules; connected to anterior region of corpus by posterodorsally directed cuticular bar widening dorsally and with pair of short, posteriorly directed "ears" extending across corpus. Anterior region of corpus weakly cuticularized, lateral margins granular in appearance, extending posteriad to join heavily cuticularized and deeply brownish "handle" portion of body and crura. Proximally fused crura, bifurcating from handle region of corpus and extending posteriad dorsal to cloacal aperture; crura smooth, lacking dorsally directed clawlike extensions, but with weakly developed ventrally directed tooth-like, triangular prominences near distal extremity of each leg. Distal ends of legs enclosed in trilobed, membranous, weakly cuticularized extension of telamon. In lateral view gubernaculum is sinuous, with a kink near origin of legs, handle directed slightly ventrally and remaining region of corpus, anterior to handle, extending anterodorsally.

Larval stages

First-stage larvae present in lungs and rectal feces; no meristic or structural differences were demonstrated (Figs. 27–29). Body slender, often coiled, with prominent, non-bifurcate, lateral alae extending from near cephalic extremity to near anus; (n = 20) 396–435 (411 ± 11.84) in length, 18–24 (22 ± 1.67) in width at base of esophagus near midbody. Esophagus long, 46–51% of body length; (n = 20) 189–212 (199 ± 6.59) long, 12–16 (14 ± 1.09) wide at base. Excretory pore (n = 20) 103–115 (109 ± 4.26) and nerve ring 91–120 (108 ± 7.05) from cephalic extremity. Genital primordium composed of 2 ovoid cells situated ventral to intestine in posterior of body, (n = 20) 257–280 (269 ± 8.52) from cephalic extremity. Anus located (n = 20) 38–50 (45 ± 2.90) anterior to caudal extremity. Tail with 3 prominent cuticular folds. Proximal fold (n = 20) 11–16 (14 ± 1.61) from tip of tail; oriented at an angle to axis of body; dorsal spine originates at level of proximal fold, (n = 20) 2–3 (2.7 ± 0.34) in length. Medial fold perpendicular to axis of body, lacking diminutive dorsal and ventral spines. Distal fold, perpendicular to body axis, near termina-

Figs. 27–34. *Umingmakstrongylus pallikuukensis* gen.nov. et sp.nov. Larvae in first and third stages. Fig. 27. Entire view of a first-stage larva in lateral view, showing the structure of the esophagus and intestine and the position of the nerve ring, excretory pore, and genital primordium. Fig. 28. Tail of a first-stage larva in lateral view; note the termination of the lateral alae adjacent to the dorsal spine, and the proximal, medial, and distal cuticular folds. Fig. 29. Transverse section of a first-stage larva, showing the prominent lateral alae. Fig. 30. Third-stage larva in lateral view, showing the cuticularized buccal cavity, the structure of the esophagus and intestine, and the positions of nerve ring, excretory pore, and genital primordium. Fig. 31. Third-stage larva in lateral view at the level of the excretory pore, showing the cuticular grooves. Fig. 32. Third-stage larva in lateral view posterior to the midbody, showing the cuticular grooves. Fig. 33. Third-stage larva in transverse section (dorsal toward the top) at the level of the posterior esophagus; note the cuticular grooves in lateral fields, and the massive excretory system. Fig. 34. Third-stage larva in transverse section at the level of the genital primordium.



tion of tail; tail spike (n = 20) 2.5–5.0 (3.5 ± 0.62) long, extends posteriad from distal fold to caudal apex. Tail region kinked at basal and medial folds, giving sinuous appearance to tail.

Third-stage larvae, from experimental infection in the slug *D. reticulatum*, robust, curved ventrally, (n = 10) 514–600 (560 ± 33.64) long; 39–60 (47 ± 7.0) wide at base of esophagus (Figs. 30–34). Length of esophagus 33–39% of body length; (n = 10) 181–214 (200 ± 11.71) long, 18–26 (23 ± 3.29) wide at base. Excretory pore (n = 10) 109–127 (118 ± 5.01) and nerve ring (n = 10) 93–106 (99 ± 4.23) from cephalic extremity. Massive excretory system evident laterally. Genital primordium ovoid, (n = 10) 318–388 (361 ± 22.74) from anterior. Anus situated (n = 10) 26–34 (31 ± 2.88) anterior to apex of broad and bluntly rounded tail. Cuticle with discontinuous system of surficial, parallel, irregular grooves in lateral fields extending from level of cephalic extremity to near tail; 5–7 in each field in anterior, 7–9 in posterior.

HOST: Type and only known host, muskox, *Ovibos moschatus moschatus* (Zimmermann).

HABITAT: Adult males and females, with eggs and first-stage larvae, contained in tissue cysts of host origin, distributed throughout the lung tissue.

LOCALITY: Type locality Cox Lake, Northwest Territories, Canada (ca. 68°54′N, 116°38′W); also from the vicinity of the lower Coppermine, Rae, and Richardson rivers, adjacent to Richardson Bay and western Coronation Gulf, Northwest Territories, Canada. Originally collected in 1988 near the Rae River valley at ca. 68°17′N, 116°05′W.

SPECIMENS: Holotype male, Canadian National Museum of Nature, CMNP 1995-0040, and allotype female, CMNP 1995-0041, from type host and locality on 12 April 1994 by E.P. Hoberg, A. Niptanatiak, J. Nishi, and R. Lamont. Paratype specimens from the type host and locality deposited in the U.S. National Parasite Collection include 6 complete males (in 6 vials), USNPC 84826; 23 caudal extremities of males (2 vials), USNPC 84827; 14 caudal extremities of females (2 vials), USNPC 84828; and 28 cephalic extremities (1 vial), USNPC 84829. Other paratypes were derived from material collected on 20 February 1992 from *O. moschatus* in the Rae River valley by A. Gunn and include 1 complete male, CMNP 1995-0042; 9 caudal extremities each of males and females and 12 cephalic extremities deposited as CMNP 1995-0043. Included as paratypes are a vial of first-stage larvae derived from lung tissue collected on 20 February 1992, USNPC 84830; and a vial of third-stage larvae from an experimental infection in *D. reticulatum*, USNPC 84831. Vouchers include fragmented specimens, first-stage larvae, and 4 cysts collected on 20 February 1992 (3 vials), USNPC 84832; 25 intact cysts, fragmented specimens, and first-stage larvae collected from the type host and locality in 1994 (15 vials, 1 collection jar), USNPC 84833; and 2 vials of first-stage larvae from lungs of the type host and locality in 1994, CMNP 1995-0044. Histological sections of cysts and parasites included material collected from *O. moschatus* by A. Gunn in the Rae River valley: 4 slides (WCVM N90-972) collected on 27 February 1990, USNPC 84834; and 4 slides (WCVM N90-3185) collected on 25 July 1990, USNPC 84835. Additional histological specimens, fixed lung tissue, and cysts from collections conducted from 1988 through 1994 in the Coppermine region are maintained in the pathology collection at WCVM, Saskatoon, Saskatchewan.

ETYMOLOGY: The generic name is derived from *umingmak*, Inuinnaqtun for "muskoxen" (Inuinnaqtun is the dialect of the Inuit in the Kitikmeot Region, or the central Arctic), and "strongylus" for the strongylate nematodes. The specific name refers to the locality of collection and is derived from *Pallik*, the Inuinnaqtun name for the geographic region surrounding the eastern watershed of the Rae and Richardson rivers, and *kuuk*, the Inuinnaqtun word for "river." This binomial is in recognition of the contributions by the Inuit to biological research in the Arctic.

Comments

According to Boev (1975) and Anderson (1978), 12 genera are recognized in the Protostrongylidae; Boev (1975) would refer these to six subfamilies, although a phylogenetic basis has yet to be established for their recognition. Generic limits in the Protostrongylidae may be poorly defined. Concepts for some taxa may include combinations of putative primitive and derived characters, and extensive variation in some "diagnostic" attributes can be recognized (e.g., the gubernaculum in species of *Varestongylus* Bhalerao, 1932; the form of the bursa and provagina in species of *Protostrongylus* Kamensky, 1905). Consequently, validation of genera within the family must eventually be considered within a phylogenetic framework. However, within the current systematic context for the family, *Umingmakstrongylus* gen.nov. is distinguished from all protostrongylids on the basis of specific structural characters of the bursa, spicules, gubernaculum, and telamon in males, the absence of a provagina in females, and the form of the tail in first-stage larvae.

Umingmakstrongylus pallikuukensis gen.nov. et sp.nov. is referred to the subfamily Muelleriinae Skrjabin, 1933 on the basis of criteria presented by Boev (1975) and thus shares some characters with species in the genera *Cystocaulus* Schulz, Orlow, and Kutass, 1933 and *Muellerius* Cameron, 1927. Primary attributes for placement in this subfamily include a reduced telamon composed only of a transverse plate; a trifurcate, elongate dorsal ray; spicules that are equal to subequal and with a characteristic joint near midlength; and first-stage larvae with a dorsally directed spine at the proximal fold of the tail.

Based on characters of adult males and females and first-stage larvae (Boev 1975; Anderson 1978), *Umingmakstrongylus* differs from *Muellerius*. In the former the caudal end of the male is relatively straight and not tightly spiraled, and the bursa is well-developed, rounded, and asymmetrically bilobate with anterior and posterior incisions and a stalk-like dorsal ray. The spicules are massive and not branched distally at their tips. The telamon is highly reduced, being limited only to the distal transverse plate, and the gubernaculum is complex rather than being composed of paired plates. In the female, the provagina is absent. Although of lesser significance, adult specimens of *U. pallikuukensis* are substantially larger than any nematodes referred to the genus *Muellerius*. The tail of the first-stage larva has 3 rather than 2 cuticular folds and lacks dorsally and ventrally directed spines on the tail spike.

Specimens of *U. pallikuukensis* appear morphologically most similar to those of species referred to the genus *Cystocaulus* (see Schulz et al. 1933; Gerichter 1951; Rose 1961;

Boev 1957, 1975; Anderson 1978). Only specimens of *C. ocreatus* approach the dimensions reported for males of *U. pallikuukensis*, but the range of lengths in males and females of the former is only 18–90 and 30–160 mm, respectively (Boev 1975). Males of *Umingmakstrongylus* differ considerably from those of *Cystocaulus* in possessing a distinctly bilobate, often asymmetric, bursa with anterior and posterior incisions. The origins of the externodorsal rays are independent and well separated from the base of the dorsal ray. The paired crurae of the gubernaculum have ventrally directed tooth-like projections distally, but lack dorsally directed clawlike extensions. However, the capitulum of the gubernaculum is complex in both *Umingmakstrongylus* and *Cystocaulus*, with paired anchorlike ears ventrally enveloping the spicules and paired dorsal ears projecting distally over the corpus (Schulz et al. 1933). The telamon in *Umingmakstrongylus* is highly reduced and lacks a proximal transverse plate. The distal plate in *Umingmakstrongylus* has paired projections directed posteriad, whereas in *C. ocreatus*, processes are directed anteriad from the telamon. In both genera there is a weakly cuticularized trilobate membrane extending from the telamon, which appears as a troughlike structure surrounding the distal crurae of the gubernaculum (Boev 1975). Spicules of *U. pallikuukensis* have well-developed membranous alae but are not split distally. In females of *Umingmakstrongylus* the provagina is absent. The tail of the first-stage larva has 3 cuticular folds; these are defined as proximal, medial, and distal, thus apparently being unique among the Protostrongylidae. The medial cuticular fold is considered homologous in position to the distal fold in *Cystocaulus* and species of other genera where it is present (see Gerichter 1951; Boev 1975); ventrally and dorsally directed spines extending from the medial cuticular fold are lacking. However, it is clear that more critical examination of the structure of the tail in first-stage larvae of various protostrongylids is warranted. Additionally, fields of lateral grooves on the third-stage larvae have not been previously described among the protostrongylids.

Cuticular pores anterior and ventrolateral to the anus in females of *U. pallikuukensis* apparently have not been reported previously among the Metastrongyloidea. The papilliform structures appear homologous to the "perivulval pores" described by Lichtenfels et al. (1995) among some trichostrongylids, although in these nematodes they are usually situated in a dorsolateral position. In specimens of *Mecistocirrus digitatus* (Linstow, 1906) these pores are typically located posterior to the vulva and may be adjacent to the anus (Lichtenfels et al. 1995). Lichtenfels et al. (1995) considered perivulval pores to be a form of postdeirid, cuticular–sensory structures that may be widespread among the Secernentea. However, it has yet to be established whether perivulval pores have a sensory or excretory function. In specimens of *U. pallikuukensis* these papillae appear confluent with a well-defined duct system that extends anteriad within each massive lateral chord. They are not considered to be of taxonomic importance in the current study, as they are likely to be a widespread but obscure character among strongylate and other nematodes; papilliform structures were not observed in the posterior region of the body in either first- or third-stage larvae in the present study.

Discussion

Umingmakstrongylus pallikuukensis gen.nov. et sp.nov. is the first protostrongylid to be described from *Ovibos moschatus*. It is clearly differentiated from other protostrongylids on the basis of morphological attributes of adult males and females and first-stage larvae (Boev 1975; Anderson 1978) as well as the characteristic lesions associated with infection in the definitive host. Preliminary studies have indicated that the prevalence and intensity of infection are high in muskoxen from the region of the Rae and Richardson rivers, N.W.T. (Gunn et al. 1991; Gunn and Wobeser 1993).

The discovery of this apparently pathogenic nematode may influence attempts to reestablish muskoxen across their historic range in the Holarctic (Gunn 1982; Alendal and Helle 1983). Ramifications of potential introductions of this parasite with muskoxen can be considered within a framework provided by contemporary distributions of hosts and parasites, host associations, epizootiology, and parasite behavior (see Woodford and Rossiter 1994). The occurrence and apparently limited geographic distribution of *U. pallikuukensis* are enigmatic, but may be explained in the context of the biogeographic history of muskoxen in the Arctic. These points are addressed in detail in the following discussion.

Distribution of lungworms

Prior to recognition of *U. pallikuukensis*, records of adult protostrongylid nematodes from muskoxen in the Holarctic region were rare or unsubstantiated. First-stage larvae of an unidentified protostrongylid were recovered from the feces of two animals from a small herd in Sweden (Alendal and Helle 1983). Although these were thought to be similar to *Muellerius* sp., recent studies have indicated that they may be a species of *Elaphostrongylus* Cameron, 1931 (see Holt et al. 1990). Additionally, Stéen et al. (1994) reported on electrophoretic comparisons of protostrongylids in cervids, and in muskoxen from Sweden. Similarity was demonstrated among larvae of *Varestrongylus alces* Demidova and Naumitscheva, 1953 from *Alces alces* (Linnaeus) and those from *O. moschatus* and *Capreolus capreolus* (Linnaeus). The latter may support the contention that the presence of protostrongylids in muskoxen introduced to Scandinavia resulted from transfer of parasites from cattle or cervids (Alendal and Helle 1983).

In contrast, the only species of lungworm reported from muskoxen in the Nearctic region has been the trichostrongyloid *Dictyocaulus viviparus* (Bloch, 1782) (also including unidentified *Dictyocaulus* sp.). In the Canadian Arctic, this nematode was found in naturally infected muskoxen from the Northwest Territories, including the Thelon and Baker Lake region (Gibbs and Tener 1958); Bathurst Inlet (Samuel and Gray 1974); southeastern Victoria Island and Banks Island (Rowell 1989; Gunn et al. 1991). In Sweden and Norway it was thought to have been acquired from sheep, reindeer, or caribou on common pasture (Alendal and Helle 1983). Currently there are no records of lungworms from the Canadian High Arctic islands of Devon and Ellesmere (Webster and Rowell 1980), East and West Greenland (Korsholm and Olesen 1993; Alendal and Helle 1983) or from the Taimyr Peninsula in the Siberian Arctic (Rudkovskii 1991).

It is important to note that *Dictyocaulus* sp., with a direct life cycle, is a relatively common parasite in the High Arctic, based on a large number of muskoxen examined post mortem for lungworms. Since 1981, several thousand animals have been examined during commercial hunts on Banks Island (Gunn et al. 1989; Rowell 1989), with no indication of infection by *U. pallikuukensis*. Gunn et al. (1991) necropsied 152 adult muskoxen from southeastern Victoria Island. Lungs were palpated for nodules and the bronchioles dissected, thus it is unlikely that *Umingmakstrongylus* would have escaped detection. The latter surveys and a review of parasitological studies of muskoxen at high latitudes in the Holarctic (Alendal and Helle 1983) indicate an apparent absence of protostrongylids in the Canadian Arctic islands and Greenland. This is strong circumstantial evidence of a restricted geographic range for *U. pallikuukensis* in the Coppermine region. Evaluation of this hypothesis will depend on examination of populations of muskoxen on the mainland to the west of Coppermine (toward Great Bear Lake and the delta of the Mackenzie River) and those in the region of Queen Maud Gulf (east of Coppermine), which have not been previously studied. Infections of *U. pallikuukensis* were not found in muskoxen from one area in the eastern Queen Maud Gulf.

Comparison of lesions

Lesions associated with *U. pallikuukensis* are considered to be pathognomonic (Figs. 1–5). The large cysts in the lung tissue may contain reproductively active adults in addition to eggs and first-stage larvae, or degenerate nematodes, in a dense matrix. Preliminary studies by Gunn and Wobeser (1993) suggested that lesions associated with *U. pallikuukensis* were similar to those of *Muellerius capillaris*. However, more extensive evaluation has indicated that cysts described for *U. pallikuukensis* are structurally distinct from lesions typical of *M. capillaris* and *C. ocreatus*.

In *M. capillaris* two types of lesions, "brood nodules" and "worm nodules," have been described (Boch and Nürnberg 1962; Sedlmeier et al. 1969) The former are often several centimetres in greater diameter and the adult parasites are found in the alveoli. Some brood nodules also contain eggs and first-stage larvae, indicative of reproductive activity, with larvae also present in the bronchioles. Brood nodules are found primarily beneath the caudodorsal surface of the lungs, where they stimulate a diffuse inflammatory reaction without cyst formation (Sedlmeier et al. 1969). A worm nodule contains a small number of adult parasites that show no evidence of reproductive activity and appear to be degenerate, or dead and calcified, enclosed in a cyst 1–2 mm in diameter. Such lesions may be widely distributed beneath the pleural surfaces of the lungs, including within brood nodules (Sedlmeier et al. 1969). Lesions associated with *C. ocreatus* are generally similar to those of *M. capillaris* (see Rose 1961; Sedlmeier et al. 1969). In contrast to these Muelleriinae, reproductively active adults, eggs, and viable first-stage larvae of *U. pallikuukensis* occur in large well-defined cysts.

Pathogenesis associated with infection of *U. pallikuukensis* is severe (Gunn and Wobeser 1993). Cysts are space-occupying lesions, and appear to cause only local inflammation, the greatest effect being displacement and compression of tissue (Figs. 2, 4, and 5). Hosts may be debilitated by heavy infections. Consequently, heightened levels of (*i*) direct mortality attributed to pneumonia and (*ii*) indirect mortality due to impaired breathing and endurance, leading to predation by *Ursus arctos*, may be expected (Gunn 1994; Gunn et al. 1991; Gunn and Wobeser 1993). Although the discovery of this lungworm coincided with a substantial decline in the population of the Coppermine herd from an estimated 1800 ± 290 (SE) in 1988 to 970 ± 340 in 1994 (Gunn 1994; J. Nishi, unpublished data, 1995), the occurrence of *U. pallikuukensis* has not yet been linked to this population trend.

Of a sample of 53 hunter-killed muskoxen in 1989–1990, 92.5% were infected with *U. pallikuukensis*. Young animals typically harbor infections of low intensity (e.g., a yearling with 16 cysts and 3-year-old animals with 11 and 26 cysts reported herein), whereas old, mature bulls were more heavily parasitized (maximum of 258 cysts in one host) (Gunn et al. 1991). Infections appear cumulative and age- and sex-specific patterns may occur, with the greatest intensity observed in old bulls and lower levels in females and calves. Polley (1987) previously reported on the occurrence of cumulative infections of *M. capillaris* in sheep.

Transmission

From experimental infections of the slug *Deroceras reticulatum* and development of apparently viable third-stage larvae in this molluscan host it is inferred that the life cycle of *U. pallikuukensis* is similar to that of other protostrongylids. It would be expected that in the Coppermine region, an intermediate host is required for transmission. Consequently, infections of higher intensity in males may be explained by food habits and foraging behavior (Gunn et al. 1991). Older bulls typically feed in smaller wet sedge meadows, along creeks, and around lakes, likely habitat for the putative intermediate host. Additionally, adult bulls ingest a greater quantity of forage than animals of other age-classes, which could influence the intensity of infection if it is related to frequency of exposure (Gunn et al. 1991).

Completion of the life cycle may be limited to a narrow time frame as a function of the development rates of larvae, the temperature and moisture level of microhabitats, and the distribution of potential intermediate and definitive hosts. In the Arctic, microhabitats at the soil surface are often significantly warmer than general ambient conditions (see Nelson 1983). Thus, the role of temperature as a limiting factor for development in otherwise severe environments requires examination. Additionally, if transmission is linked to rates of development of third-stage larvae, then increases in global temperature could influence the distribution of this parasite.

Transmission of *U. pallikuukensis* is potentially restricted to the summer, when muskoxen are usually found in moist habitats, particularly river valleys and seepage meadows, poorly drained tracts, and areas of late snow (Gunn 1982). Parturition occurs between mid-April and mid-June, and although calves are highly precocious and will begin feeding on vegetation within a week of birth, abiotic factors controlling the availability of infected intermediate hosts and larvae could limit successful transmission.

In the Arctic, transplacental migration resulting in pre-

natal infection should also be considered. Gunn and Wobeser (1993) reported patent infections in 3-month-old calves, which suggests parasite transmission in utero. However, this route requires further investigation. Infection of term fetuses has been reported for other protostrongylids, notably *Protostrongylus stilesi* Dikmans, 1931 in *Ovis canadensis* Shaw, in which significant losses are attributed to this nematode (Forrester 1971; Hibler et al. 1972, 1974). Low survivorship of calves in the muskox population of the Coppermine region in recent years should be examined from this perspective (Gunn 1994).

Alternative definitive hosts

Protostrongylids are apparently unknown from *Rangifer tarandus* (Linnaeus) in the Coppermine region (Gunn et al. 1991). Other bovids are absent, and moose are uncommon in the area. The arctic hare, *Lepus arcticus* Ross, is the only other common medium-sized herbivore in the region (Banfield 1974). Species of *Protostrongylus* have been the only lungworms reported from leporids, and none are known from the Arctic (Boev 1975). This information supports the contention that *U. pallikuukensis* is limited to muskoxen and is unlikely to parasitize an assemblage of mammalian herbivores in the Arctic. There are no other possible cervid, bovid, or lagomorph hosts in the region that are contemporary, although an extensive fauna existed in the Arctic and Sub-Arctic during the Pleistocene (Kurtén 1968; Kurtén and Anderson 1980; Guthrie 1982).

Historical perspective

Muskoxen represent a relictual element of a mammalian fauna that dominated the Holarctic region during the Pliocene and Pleistocene (Kurtén and Anderson 1980). *Ovibos* Linnaeus originated on the tundra steppes of central Siberia in the Late Pliocene. Dispersal into Alaska, as *O. moschatus*, occurred during the late Illinoian (late Riss) less than 200 ka BP (Kurtén 1968; Kurtén and Anderson 1980). *Ovibos* attained a broad Holarctic distribution during the Pleistocene. In North America, muskoxen were found south of the Laurentide ice and also apparently survived full glacial conditions in isolated arctic refugia during the late Pleistocene (e.g., 80 or ca. 20–18 ka BP at glacial maxima in the Wisconsin) (Macpherson 1965; Harington 1961; Gunn 1982; Matthews 1979).

The contemporary geographic range of muskoxen has been determined by local extinctions (Gunn 1982). Extinction of *O. moschatus* in the Palearctic occurred after termination of the Pleistocene, and muskoxen continued to be present on the Taimyr Peninsula at 3 ka BP (Kurtén and Anderson 1980; Stuart 1991). During the Holocene, populations were present in the High Arctic islands of Canada and East Greenland. However, many populations on mainland Canada were locally extirpated during the 20th century as a result of hunting. Those in Alaska were eliminated at the end of 19th century (Gunn 1982). Recovery has occurred in some areas of Canada (Barr 1991) and over the past 60 years animals have been reintroduced, with varying success, to former range in Scandinavia (Alendal and Helle 1983), Russia (Rudkovskii 1991), and Alaska (Smith 1989). *Umingmakstrongylus pallikuukensis* may have been more common and geographically widespread in the Nearctic region during this century, but was eliminated coincidentally with hunting of its hosts. This possibility reinforces the necessity to provide control measures against inadvertent reintroduction of parasites with translocated muskoxen.

Local extirpation in the Nearctic region and broad extinction in the Palearctic region thus may account for an apparently limited distribution of *U. pallikuukensis* in the Coppermine region. The environmental setting, in the low Arctic, may be conducive to continuity of the life cycle for this parasite, in that suitable intermediate hosts, definitive hosts, and the parasite coexist. Additionally, the Coppermine herd has been historically isolated from domesticated ruminants. Caribou of the Bluenose herd migrate through the area, but lungworms have not been reported from hunter-killed animals (Gunn et al. 1991). Muskoxen of the Coppermine region apparently do not interchange with adjacent herds to the east (Bathurst Inlet, Queen Maud Gulf), west (north of Great Bear Lake), or north (Banks Island or Victoria Island across the Coronation Gulf) (Case et al. 1989). Muskoxen were absent or extremely rare in the Rae–Richardson drainage following extirpation across the low Canadian Arctic in the late 19th century. Muskoxen were seen in this drainage in the mid-1960s for the first time, and populations expanded during the 1970s and 1980s (Gunn 1994). Recolonization of this region possibly occurred from west of Bluenose Lake. Thus, if the parasite is more widespread, this might be a logical area to survey.

In the High Arctic islands of Canada and in Greenland, *U. pallikuukensis* appears to be absent in *O. moschatus wardi* Allen. The northern subspecies of muskox, a result of Pleistocene vicariance during the Wisconsin and reinvasion from a Pearyland refugium (Harington 1961; Macpherson 1965), historically may not have been infected. Alternatively, severe environmental conditions and unsuitable habitat could limit transmission, either directly because of mortality of larvae or indirectly via elimination of intermediate hosts at high Arctic latitudes. This agrees with Danks' (1981, 1992) contention that ecological factors are the primary determinants (limiting factors) of the contemporary ranges of arctic invertebrates. Although the nematode once may have had an extensive distribution in the Holarctic, the Coppermine region now may represent an interglacial refuge where a relict host–parasite assemblage has persisted since the Pleistocene.

Additionally, the existence of Pleistocene glacial refugia at the MacKenzie Delta and on Banks Island during the late Wisconsin about 20 ka BP (Matthews 1979) may explain the continuity of a muskox–parasite assemblage that secondarily became confined to isolated postglacial refugial habitats. This hypothesis must be evaluated within the context of distributional data for potential molluscan intermediate hosts and muskoxen, and the survivability of larval stages in arctic conditions.

The distribution of *U. pallikuukensis* in *O. moschatus* must also be considered in the context of host and parasite phylogeny and hypotheses concerning cospeciation or colonization. Currently, the closest extant relative of muskoxen appears to be *Budorcas taxicolor* Hodgson, the takin from central Eurasia (Neas and Hoffmann 1987; Wu 1989; Pasitschniak-Arts et al. 1994). The takin represents the putative sister-group for muskoxen, but several extinct genera

(e.g., *Symbos* Osgood) occurred prior to the origin of *Ovibos*. These have generally been allied within the tribe Ovibovini in the subfamily Caprinae (Thenius 1980; Pasitschniak-Arts et al. 1994). Alternatively, a relationship between muskoxen and some taxa of the tribe Rupicaprini has once again been advocated, based on molecular evidence (P. Groves, personal communication, 1995).

Parasitological data may not be phylogenetically informative with respect to takins and muskoxen. Patterns of host distribution for many genera of protostrongylids are poorly defined, indicating limited specificity within the family and the potential for host-switching. *Varestrongylus longispiculatus* Liu, 1989, the sole protostrongylid described from the takin (Boev 1975; Liu 1989), is morphologically dissimilar to *U. pallikuukensis*. However, other protostrongylids, notably the Muelleriinae and species of *Cystocaulus*, that share a suite of characters with *Umingmakstrongylus* are typical parasites of wild goats (*Capra* Linnaeus) and sheep (*Ovis* Linnaeus) (tribe Caprini) in Eurasia and North America (Boev 1975). Additionally, protostrongylids do not indicate affinities with the rupicaprine bovids such as *Oreamnos americanus* (de Blainville) or *Rupicapra rupicapra* Linnaeus (see Boev 1975). These patterns of host association suggest that *Umingmakstrongylus* is not a component of a coevolved fauna in bovids.

The origin of *Umingmakstrongylus* could be related to a colonization event during the Pleistocene. During glacial stages of the Wisconsin and earlier, a complex grazing community of large mammalian herbivores existed across Beringia and the Holarctic region (Guthrie 1968, 1982, 1984; Kurtén 1968; Vereshchagin and Baryshnikov 1982). In the Nearctic and Palearctic regions, muskoxen were sympatric and synchronic with a diverse assemblage of bovids (species of *Bison* Linnaeus, *Saiga* Gray, and *Ovis*), cervids (including *R. tarandus* and species of *Cervus* Linnaeus and *Alces* Gray), antilocaprids, camelids, equids, and proboscideans (Guilday 1984; Kurtén 1968; Kurtén and Anderson 1980; Stuart 1991). Extensive sympatry and high diversity of this Pleistocene megafauna suggest the potential for host-switching by parasites among herbivorous hosts. However, at the termination of the Wisconsin, climatological fluctuation and habitat disruption led to range restriction, diminished sympatry, and extinction for some species of this mammalian community (Guthrie 1982, 1984). Increased allopatry and extinction of hosts during the Holocene could have (*i*) resulted in lowered parasite faunal diversity or (*ii*) constituted a determinant of postglacial isolation and allopatric speciation of parasites. These factors may account for the origin and subsequent distributional history of *U. pallikuukensis*.

Phylogenetic analysis of the Protostrongylidae is requisite in elucidating the evolutionary and biogeographic history of *Umingmakstrongylus*. A coevolutionary history with the muskox would indicate derivation from a previous lungworm fauna characteristic of related bovids (e.g., subfamily Caprinae). In contrast, cospeciation analysis may reveal a putative history related to a colonization event and subsequent speciation during the Quaternary, based on a host-switch from arctic cervids (e.g., *R. tarandus* or *A. alces*) or bovids (*Ovis* spp.), or components of the now extinct steppe fauna of the Pleistocene.

Acknowledgments

We are indebted to John Stevenson and Ron Morrison of the Department of Renewable Resources, Government of the Northwest Territories, and the people of Coppermine, N.W.T., for their exceptional support and interest, which made this study possible. We thank John and Emily Stevenson, Ron and Julie Morrison, and Allen and Grace Niptanatiak for their generous hospitality during fieldwork in April 1994. We thank Allen Niptanatiak and Ron Lamont for their great expertise in the field and assistance in the laboratory. The Kugluktuk School and Coppermine Nursing Station are acknowledged for the loan of a dissecting microscope and lupe magnifier. Gary Wobeser and Peter Flood at WCVM, Saskatoon, provided substantial background information on the Coppermine herd. Alvin Gajadhar of Agriculture Canada, Saskatoon, shared information on the rearing of slugs and on protocols for experimental infections. Geordie Erickson, Brent Wagner, and Susan Kutz conducted work on infections in the intermediate host at WCVM. Susan Kutz also provided data and first-stage larvae from lungs and feces from collections in November 1994. At the Agricultural Research Service, Beltsville, Maryland, Patricia Pilitt prepared transverse sections of nematodes and Charles Murphy conducted the SEM. Robert Nelson discussed ideas on Pleistocene refugia and the environmental setting of the Arctic coast. Lawrence Kaplan and Robert Rausch assisted with grammar and spelling in Inuinnaqtun. Critical review of the manuscript was kindly provided by Thomas Platt and Ramon Carreno. This paper constitutes Contribution No. 6 of the PanArctic Biota Project.

References

Alendal, E., and Helle, O. 1983. Helminth parasites of muskoxen *Ovibos moschatus* in Norway incl. Spitsbergen and in Sweden, with a synopsis of parasites reported from this host. Fauna Norv. Ser. A, **4**: 41–52.

Anderson, R.C. 1978. Keys to the genera of the superfamily Metastrongyloidea. No. 5. *In* CIH keys to the nematode parasites of vertebrates. *Edited by* R.C. Anderson, A.G. Chabaud, and S. Willmott. Commonwealth Agricultural Bureaux, Farnham Royal, England.

Banfield, A.W.F. 1974. The mammals of Canada. University of Toronto Press, Toronto.

Barr, W. 1991. Back from the brink: the road to muskox conservation in the Northwest Territories. Komatik Ser. 3, Arctic Insitute of North America, Calgary, Alberta.

Boch, J., and Nürnberg, H. 1962. Lungenwürmer der Schafe. Vet. Med. Nachr. **2**: 101–107.

Boev, S.N. 1957. Lung nematodes of hoofed animals in Khazakhstan. Academy of Sciences of the Kazakh SSR, Institute of Zoology, Alma-Ata. [English translation by the Israel Program for Scientific Translations, Jerusalem, 1962.]

Boev, S.N. 1975. Protostrongylids. Fundamentals of Nematodology. Vol. 25. Helminthological Laboratory, Academy of Sciences of the USSR, Moscow. [English Translation by the U.S. Department of Agriculture, Washington, D.C., and Amerind Publishing Co., New Delhi, 1984.]

Case, R., Gunn, A., and Jackson, F. 1989. Status and management of muskoxen in the Northwest Territories. Can. J. Zool. **67**: A16–A22.

Danks, H.V. 1981. Arctic arthropods: a review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada, Ottawa.

Danks, H.V. 1992. Arctic insects as indicators of environmental change. Arctic, **45**: 159–166.

Forrester, D.J. 1971. Bighorn sheep lungworm pneumonia complex. *In* Parasitic diseases of wild mammals. *Edited by* J.W. Davis and R.C. Anderson. Iowa State University Press. Ames. pp. 158–173.

Gerichter, C.B. 1951. Studies on the lung nematodes of sheep and goats in the Levant. Parasitology, **41**: 166–183.

Gibbs, H.C., and Tener, J.S. 1958. On some helminth parasites collected from the musk ox (*Ovibos moschatus*) in the Thelon Game Sanctuary, Northwest Territories. Can. J. Zool. **36**: 529–532.

Guilday, J.E. 1984. Pleistocene extinction and environmental change: case study of the Appalachians. *In* Quaternary extinctions: a prehistoric revolution. *Edited by* P.S. Martin and R.G. Klein. University of Arizona Press, Tuscon. pp. 250–258.

Gunn, A. 1982. Muskox, *Ovibos moschatus*. *In* Wild mammals of North America: biology, management and economics. *Edited by* J.A. Chapman and G.A. Feldhamer. Johns Hopkins University Press, Baltimore, Md. pp. 1021–1035.

Gunn, A. 1994. Distribution and abundance of muskoxen west of Coppermine. File Rep. No. 109, Department of Renewable Resources, Government of the Northwest Territories, Coppermine.

Gunn, A., and Wobeser, G. 1993. Protostrongylid lungworm infection in muskoxen, Coppermine, N.W.T., Canada. Rangifer, **13**: 45–47.

Gunn, A., Shank, C., and Caughley, G. 1989. Report of the workshop on management options for rapidly expanding muskox populations using Banks Island as an example. Can. J. Zool. **67**: A37–A38.

Gunn, A., Leighton, T., and Wobeser, G. 1991. Wildlife diseases and parasites in the Kitikmeot Region, 1984–1990. File Rep. No. 104, Department of Renewable Resources, Government of the Northwest Territories, Coppermine.

Guthrie, R.D. 1968. Paleoecology of the large-mammal community in interior Alaska during the late Pleistocene. Am. Midl. Nat. **79**: 346–363.

Guthrie, R.D. 1982. Mammals of the mammoth steppe as paleoenvironmental indicators. *In* Paleoecology of Beringia. *Edited by* D.M. Hopkins, J.V. Matthews, Jr., C.E. Schweger, and S.B. Young. Academic Press, New York. pp. 307–326.

Guthrie, R D. 1984. Mosaics, allelochemics and nutrients: an ecological theory of late Pleistocene megafaunal extinctions. *In* Quaternary extinctions: a prehistoric revolution. *Edited by* P.S. Martin and R.G. Klein. University of Arizona Press, Tucson. pp. 259–298.

Harington, C.R. 1961. History, distribution and ecology of the muskoxen. M.Sc. thesis, McGill University, Montréal, Que.

Hibler, C.P., Lange, R.E., and Metzger, C.J. 1972. Transplacental transmission of *Protostrongylus* spp. in bighorn sheep. J. Wildl. Dis. **8**: 389.

Hibler, C.P., Metzger, C.J., Spraker, T.R., and Lange, R.E. 1974. Further observation on *Protostrongylus* sp. infection by transplacental transmission in bighorn sheep. J. Wildl. Dis. **10**: 39–41.

Holt, G., Berg, C., and Haugen, A. 1990. Nematode related spinal myelomeningitis and posterior ataxia in muskoxen (*Ovibos moschatus*). J. Wildl. Dis. **26**: 528–531.

Korsholm, H., and Olesen, C.R. 1993. Preliminary investigations on the parasite burden and distribution of endoparasite species of muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus groenlandicus*) in West Greenland. Rangifer, **13**: 185–189.

Kurtén, B. 1968. Pleistocene mammals of Europe. Weidenfeld and Nicholson Publishers, London.

Kurtén, B., and Anderson, E. 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Lichtenfels, J.R., Wergin, W.P., Murphy, C., and Pilitt, P.A. 1995. Bilateral, perivulval cuticular pores in trichostrongylid nematodes. J. Parasitol. **81**: 633–636.

Liu, S.X. 1989. A newly identified species of protostrongylid lungworm in takin. [In Chinese, with English summary.] Acta Zool. Sin. **14**: 269–272.

Macpherson, A.H. 1965. The origin of diversity in mammals of the Canadian Arctic tundra. Syst. Zool. **14**: 153–173.

Matthews, J.V., Jr. 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. *In* Canada and its insect fauna. *Edited by* H.V. Danks. Mem. Entomol. Soc. Can. No. 108. pp. 31–86.

Neas, J.F., and Hoffmann, R.S. 1987. *Budorcas taxicolor*. Mamm. Species No. 277. pp. 1–7.

Nelson, R.E. 1983. New records of *Blethisa catenaria* Brown (Coleoptera: Carabidae) from the American Arctic, with notes on possible climatic tolerances. Coleopt. Bull. **37**: 168–172.

Pasitschniak-Arts, M., Flood, P.F., Schmutz, S.M., and Seidel, B. 1994. A comparison of G-band patterns of the muskox and takin and their evolutionary relationship to sheep. J. Hered. **85**: 143–147.

Polley, L. 1987. Quantitative observations on intrapulmonary populations of *Muellerius capillaris* (Mueller, 1889) Cameron, 1927, in sheep. J. Parasitol. **73**: 234–236.

Rose, J.H. 1961. Three lungworms recently recorded from British sheep. Res. Vet. Sci. **2**: 253–258.

Rowell, J.E. 1989. Survey of reproductive tracts from female muskoxen harvested on Banks Island, N.W.T. Can. J. Zool. **67**: A57.

Rudkovskii, A.I. 1991. Endoparazity ovtsebykov na Taiimyre. Veterinariya (Mosc), **5**: 41–44.

Samuel, W.M., and Gray, D.R. 1974. Parasitic infection in muskoxen. J. Wildl. Manage. **38**: 775–782.

Schulz, R.E., Orlow, I.W., and Kutass, A.J. 1933. Zur Systematik der Subfamilie Synthetocaulinae Skrj. 1932 nebst Beschreibung einiger neuer Gattungen und Arten. Zool. Anz. **15**: 303–310.

Sedlmeier, H., Schiefer, B., and Menschek, H. 1969. Möglichkeiten einer Differenzierung von Lungewurminfektion des Schafes im histologischen Schnittpräparat: zugleich ein Beitrag zur Frage der Enstehung der Lungenadenomatose des Schafes durch Parasiten. Zentrbl. Veterinaermed. **16**: 143–157.

Smith, T.E. 1989. The status of muskoxen in Alaska. Can. J. Zool. **67**: A23–A25.

Stéen, M., Persson, S., and Hajdu, L. 1994. Protostrongylidae in Cervidae and *Ovibos moscatus*: a clustering based on isoelectric focusing on nematode proteins. Appl. Parasitol. **35**: 193–206.

Stuart, A.J. 1991. Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. Biol. Rev. Camb. Philos. Soc. **66**: 453–562.

Thenius, E. 1980. Grundzüge der Faunen- und Verbreitungsgeschichte der Säugetiere. Gustav Fischer Verlag, Stuttgart.

Vereshchagin, N.K., and Baryshnikov, G.F. 1982. Paleoecology of the mammoth fauna in the Eurasian Arctic. *In* Paleoecology of Beringia. *Edited by* D.M. Hopkins, J.V. Matthews, Jr., C.E. Schweger, and S.B. Young. Academic Press, New York. pp. 267–279.

Webster, W.A., and Rowell, J. 1980. Some helminth parasites from the small intestine of free-ranging muskoxen *Ovibos moschatus* (Zimmermann) of Devon and Ellesmere Islands, Northwest Territories. Can. J. Zool. **58**: 304–305.

Woodford, M.H., and Rossiter, P.B. 1994. Disease risks associated with wildlife translocation projects. *In* Creative conservation: interactive management of wild and captive animals. *Edited by* P.J.S. Olney, G.M. Mace, and A.T. Feistner. Chapman and Hall, London. pp. 178–200.

Wu, J.-Y. 1989. The systematics and distribution of the takin. Can. J. Zool. **67**: A10–A13.